

THE MILLIPED GENUS *CROATANIA*
(POLYDESMIDA: XYSTODESMIDAE)

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The xystodesmid milliped fauna of the lowland regions of the Carolinas is sparse in comparison to that of the southern Appalachian Mountains. *Apheloria tigana* Chamberlin is dominant in the fall zone region of North Carolina (Shelley 1977), and *Sigmorina latior* (Brölemann) (three subspecies plus intergrades) ranges through piedmont North Carolina to the southern Coastal Plain of South Carolina (Shelley 1976). *Cleptoria macra* Chamberlin is known from the counties of Greenville and Newberry, S.C. (Hoffman 1967), and *Pachydesmus crassicutis incurtus* Chamberlin occurs from the inner Coastal Plain and Piedmont of South Carolina to the Kings Mountain region (Cleveland and Gaston counties) of North Carolina (Shelley and Filka 1977). Other lowland xystodesmids include *Nannaria conservata* Chamberlin, *N. rutherfordensis* Shelley, and *Pleurolooma* sp. in North Carolina (Shelley 1975, 1977), and *Stelgipus agrestis* Loomis in South Carolina (Chamberlin and Hoffman 1958).

In August 1975 I discovered several xystodesmids in a moist seepage area in the Kings Mountain, N.C., region that represented an undiagnosed generic form. A year later the genus was found to be common in a variety of piedmont South Carolina biotopes ranging south to the Savannah River. Available museum specimens confirm its occurrence on islands of the extreme southern coast of the state. Four distinct species are represented, with no evidence of intergradation or development of geographic races. Accordingly, I propose the name *Croatania* for this complex, and present descriptive, ecological, distributional, and phylogenetic information.

Materials and Methods

Over 170 specimens have been examined during this study, and except for five in the personal collection of Richard L. Hoffman (RLH), all were collected by the author or an assistant and deposited in the invertebrate collection of the North Carolina State Museum (NCSM), the invertebrate catalog numbers of which are indicated in parentheses. Color and habitat observations were recorded in the field at the time of collection. Illustrations were prepared with the aid of a binocular stereomicroscope fitted with a grid reticle, and measurements were made with vernier-scale calipers of specimens lying flat, straight, and compressed.

The format for this publication is similar to the xystodesmid revisions of Hoffman, as exemplified by his work on *Cleptoria* (1967). Thus, a discussion of taxonomic characters precedes the descriptive sections, there being no prior literature to review. Discussions of ecology, distribution, and phylogenetic relationships, both generic and specific, conclude the paper. Illustrations of diagnostic features and a taxonomic key are provided to aid in determinations and establish the identities of the species.

Taxonomic Characters

Color.—The paranotal color of many xystodesmids is highly variable and a poor taxonomic character, but in *Croatania*, it is remarkably constant for each species. All specimens of *C. saluda*, for example, have red paranota, whereas both *C. catawba* and *C. simplex* display a yellowish color. There may or may not be a concolorous stripe along the anterior edge of the column, and some individuals of *C. saluda* have narrow paranotal markings covering little more than the peritremata. Two specimens of *C. catawba* have an orangish hue to the paranota, but this could not possibly be confused with the red of *C. saluda*. Thus, color affords a general basis for field identifications of the three Piedmont species; the color of *C. yemassee*, in the Coastal Plain, is unknown.

Sterna.—The postgonopodal sterna of *Croatania* are a modification of the bilobed variation described by Hoffman (1965). The true bilobed condition, producing acute subcoxal spines, is most evident on segments 8–11 of *C. catawba*, and the sterna become progressively flatter posteriorly. In the other species, the bilobed condition is only noticeable on segment eight.

The pregonopodal sterna exhibit several modifications. On the fourth segment of both sexes there is a large, ventrally directed, bilobed process (Figs. 11–15), which is most highly developed in males of *C. catawba* and *C. saluda*. Here it is longer than the widths of adjacent coxae, bent antierad distally, and divided into two lobes near the apices. In males of *C. yemassee* and *C. simplex* the structure is straight, and in the latter it is shorter than the width of the adjacent coxae and divided near mid-length. In all females the process is much shorter than the adjacent coxae and almost completely separated into two paramedian lobes (Fig. 12).

Segments five and six of males also possess sternal modifications. On segment five, between the anterior (4th) legs, is a pair of digitiform lobes which are subsimilar in all four species. Between the posterior (5th) legs there are elevated flattened areas that also do not vary appreciably between species. The sternum of segment six is recessed between the seventh legs to accommodate the distal curvature of the gonopodal telopodite. This depression is relatively shallow in *C. catawba*, *C. saluda*, and *C.*

simplex, but much deeper in *C. yemassee* due to the higher arc of its telopodite.

Gonopods.—As with most xystodesmids, the principal diagnostic structures at both the generic and species levels are the male gonopods. Neither coloration nor sternal configuration can alone distinguish *Croatania* from related genera.

Two features of the gonopods are especially important—a large prefemoral process, and an elaborate, irregularly notched expansion of the proximomedial edge of the telopodite. The latter, which imparts a bizarre, spiny appearance to the gonopods, is unique to *Croatania* and presumably a specialization. It varies in length and degree of jaggedness and is reduced and relatively inconspicuous in *C. yemassee*. The prefemoral processes of *C. catawba*, *C. saluda*, and *C. yemassee* (Figs. 1, 3, 6) are enormous, extending to or beyond the level of the tip of the telopodite, and set them apart from sympatric xystodemids. The fourth species, *C. simplex*, differs in having a reduced prefemoral process that terminates well below the level of the tip of the telopodite (Fig. 4).

Additional features of the gonopods that are diagnostically important include the degree of arch of the telopodite, the sizes of the medial and lateral subapical lobes, and the length of the solenomerite relative to the lobes. In *C. catawba* and *C. saluda* the gonopods are so similar that there is little doubt about their cogenetic status. The other two species, *C. yemassee* and *C. simplex*, differ sufficiently, however, that one could justifiably question their being congeneric with each other as well as with the more typical species. The former, in addition to a greatly reduced proximomedial expansion of the telopodite, has a much higher distal arch and more reduced subapical lobes than either *C. catawba* or *C. saluda*. The prefemoral process, however, is equivalent in size to those of the latter species, and this, plus the presence of subapical lobes and a proximomedial expansion, even though reduced, justify inclusion in the same genus.

The fourth species, *C. simplex*, is even more dissimilar, and I originally considered erecting a monotypic genus to accommodate it. As indicated above, this species is unique in having a short prefemoral process, but it is also distinguished by an elongate, acuminate solenomerite. The thin, reduced subapical lobes of the telopodite are even more inconspicuous than those of *C. yemassee*. Their presence, however, plus the well developed, notched expansion and the occasional appearance of bifurcation in the prefemoral process, which resembles the condition in *C. saluda*, are enough, in my opinion, to place the form in the same genus. This is the conservative approach, especially since *C. simplex* is known from only one locality, and additional material might provide a clearer indication of the relationship. Further discussion of relationships in *Croatania* is presented in the concluding section.

Cyphopods.—The operculum and valves of the female cyphopods of *Croatania* are small and surrounded on three sides, ventrally, anteriorly, and caudally, by the receptacle. The membrane to which the cyphopod is attached is greatly enlarged and folded, particularly on the medial side, where it protrudes through the aperture (Fig. 16). This bulging medial enlargement appears to be a fundamental part of the female anatomy, although its function is unknown. It is most highly developed in *C. catawba*, but present in females of all four species. In some individuals it contains darkened inclusions. This structure has never before been reported in the Xystodesmidae and is considered a clear indication of generic distinction for this complex. It is also further justification of congeneric status for *C. simplex*.

Croatania, new genus

Type-species.—*Croatania catawba*, new species.

Description.—A genus of moderate to large xystodesmids with the following characteristics:

Body composed of head and 20 segments in both sexes; relatively large and compact in form, W/L ratio varying from 21 to 26 percent. Head of normal appearance, smooth, polished; epicranial suture distinct, not bifid; interantennal isthmus relatively broad; genae not or moderately impressed; facial setae reduced, epicranial and interantennal absent, with or without frontal setae. Antennae extending caudad to posterior portion of third metatergite; with four antennal cones on ultimate antennomere; no other sensory structures.

Terga polished, smooth medially, becoming coriaceous near paranota; latter broad, depressed, continuing slope of dorsum; peritremata flat on anteriormost segments, becoming more distinct and elevated in midbody region; ozopores opening dorsolaterad. Prozonites generally smaller than metazonites, meeting at distinct sutural line, becoming most sharply defined at level of stricture.

Caudal segments normal for family.

Sterna variable, either flattened on postgonopodal segments or depressed medially and produced into prominent subcoxal lobes, lobed condition most prominent on eighth segment; sternum of fourth segment produced into large medial process; of fifth segment, produced into two prominent digitiform lobes between fourth legs; recessed on sixth segment between seventh legs.

Gonopodal aperture subelliptical, narrowing slightly dorsolaterad. Gonopods large, projecting forward beyond edge of aperture into sternal depression between seventh pair of legs, usually not overlapping. Coxa large, without apophysis, connected by membrane only, no sternal remnant. Prefemur small, with large prefemoral process arising on dorsal side. Telop-

odite with irregularly notched expansion along proximomedial edge, curved anteriad, apex recurved with subapical medial and lateral lobes; solenomerite curved proximad, length variable.

Cyphopods with convoluted enlargement of membrane protruding through medial portion of aperture; receptacle visible in lateral half of aperture, extending around valves; valves directed dorsad, subequal in size; operculum minute, concealed under free end of valves.

Range.—Coastal Plain and Piedmont physiographic provinces of North and South Carolina, from Lincoln Co., in south-central North Carolina, to the coastal islands of southern South Carolina (Fig. 17).

Species.—Four. Additional species may be encountered in the Piedmont province of Georgia.

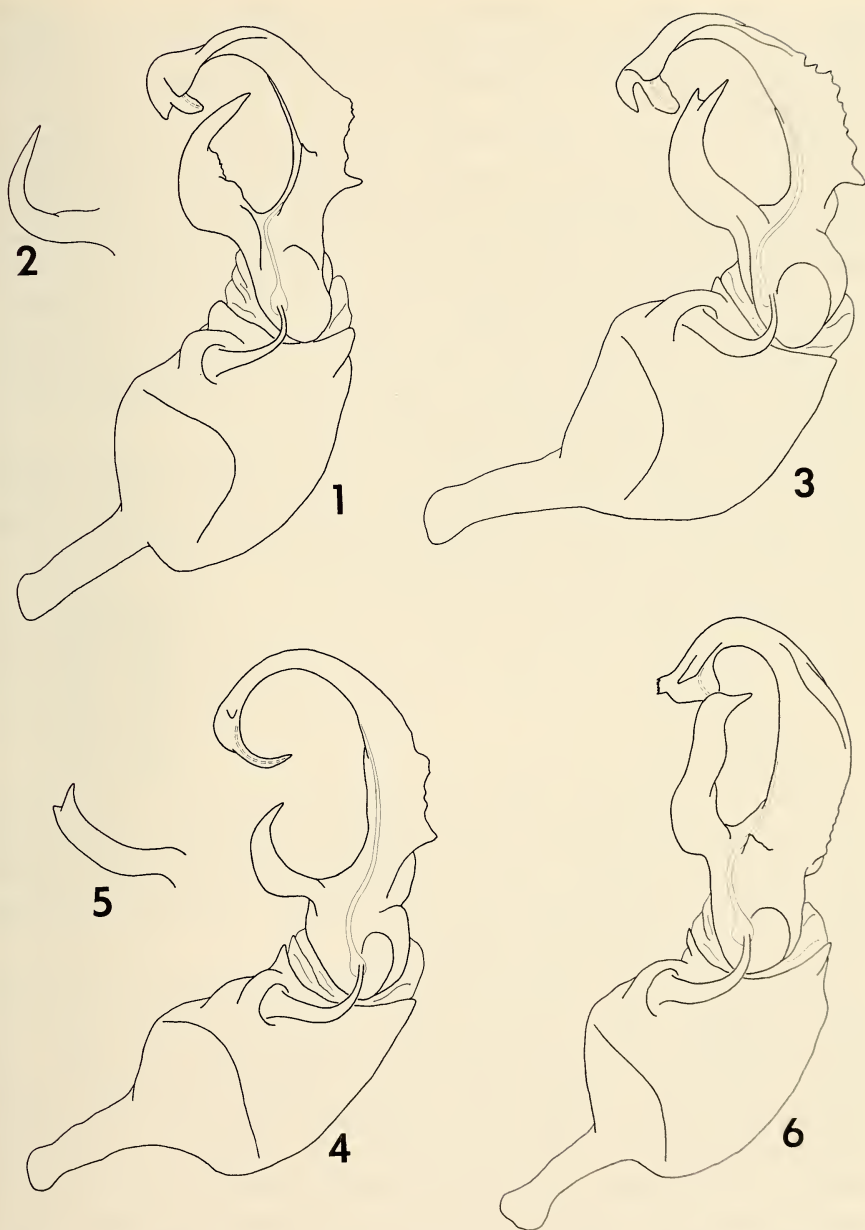
Key to Species of *Croatania* (based on adult males)

1. Prefemoral process of male gonopod large, extending to or beyond level of tip of telopodite 2
 - Prefemoral process reduced, terminating well below level of tip of telopodite; Chester Co., S.C. *simplex*, new species
2. Prefemoral process apically bifurcate; Newberry to McCormick counties, S.C. *saluda*, new species
 - Prefemoral process simple, not bifurcate 3
3. Prefemoral process subglobose basally; proximomedial edge of telopodite with conspicuous, irregularly notched expansion; arc of telopodite relatively flat and broad; distal extremity of telopodite subequal to outermost point in curvature of prefemoral process; subapical lobes of telopodite large, conspicuous; Lincoln Co., N.C. to Union Co., S.C. *catawba*, new species
 - Prefemoral process of approximately uniform width except near tip; expansion of proxiomedial edge of telopodite inconspicuous, with only small denticulations; arc of telopodite relatively short and high; distal extremity of telopodite extending beyond outermost point in curvature of prefemoral process; subapical lobes reduced, indistinct; coastal islands and outer Coastal Plain of Beaufort and Jasper counties, S.C. *yemassee*, new species

Croatania catawba, new species

Figs. 1-2, 7, 11-12, 16

Type-specimens.—Male holotype (NCSM A540) and eight male and five female paratypes collected by R. M. Shelley and J. C. Clamp, 16 August 1975, from Cleveland Co., N.C., 5.8 mi S Kings Mountain



Figs. 1-6. Left male gonopods of *Croatania* spp., medial views. 1-2, *C. catauba*; 1, Holotype; 2, Prefemoral process of specimen from Woods Ferry Recreation Center, Chester Co., South Carolina. 3, *C. saluda*, holotype. 4-5, *C. simplex*; 4, Holotype; 5, Bifurcate prefemoral process of paratype. 6, *C. yemassee*.

(town), along county road 2245, 0.1 mi N junction county road 2288. Male and female paratypes deposited in Florida State Collection of Arthropods, Zoologisch Museum Amsterdam, and personal collection of Richard L. Hoffman.

Diagnosis.—Paranota yellow, with or without yellow stripe along anterior edge of collum; sternal processes between third pair of legs of males longer than width of adjacent coxae, diverging near apices, bent anteriorly distally; postgonopodal sterna distinctly bilobed on segments 8–11; gonopods with following characteristics: prefemoral process subglobose basally, bent sharply ventrad at $\frac{2}{3}$ length; expansion of proximomedial edge of telopodite relatively short, irregularly notched; arc of telopodite relatively flat and broad; subapical lobes of telopodite large, distinct; solenomerite subequal in length to lateral lobe; distal extremity of telopodite subequal to outermost point in curvature of prefemoral process.

Holotype.—Length 50.6 mm, greatest width 11.4 mm; W/L ratio 22.5%. Paranota depressed, creating high depth/width ratio of 61.4% at midbody. Body essentially parallel sided in midbody region, tapering at both ends as indicated by following segmental widths:

Collum	8.0 mm	14th	11.0
2nd	9.2	15th	10.5
3rd	9.9	16th	9.9
4th–6th	10.7	17th	8.9
8th–12th	11.4	18th	6.4

Color in life.—Paranota bright lemon yellow, metaterga black; broad yellow stripe along anterior edge of collum, connecting with paranotal spots. Epicranium, genae, and frons black, epicranial suture and clypeus lighter; antennae brown, ultimate segment darkest. Venter and legs light brown, claws and distal ends of tarsi darker.

Head capsule smooth, polished; width across genal apices 5.3 mm; interantennal isthmus broad (1.7 mm), smooth; epicranial suture thin but distinct, terminating at level of antennae. Antennae moderately long and slender, extending to middle of paranota of third segment, becoming progressively more hirsute distally; first antennomere subglobose, 2–6 clavate, 7 short and truncate. Genae not margined laterally, trace of medial impression, ends broadly rounded and extending slightly beyond adjacent margins of cranium. Facial setae as follows: epicranial and interantennal absent; frontal 1-1; genal 3-3; clypeal about 8-8, irregularly spaced; labral about 12-12, varying in length.

Terga polished, coriaceous. Collum large, broad, extending slightly beyond ends of following tergite on each side. Paranota depressed, con-

tinuing slope of middorsum, corners rounded on segments 2-4, becoming slightly more distinct on 5-7 and progressively more pointed posteriorly due to thickening of peritremata. Peritremata virtually flat through segment 6, only slightly elevated above paranotal surface; higher and more distinct on segments 7-8. Ozopores small and indistinct, situated near middle of peritremata, opening dorsolaterad.

Sides of metazonites irregular, with several shallow, curved impressions. Strictures broad, distinct. Sternum between third pair of legs produced into large process (Fig. 11), divided apically, bent anteriorly distally, extending well beyond margins of adjacent coxae; sternum of segment 5 produced into two small digitiform lobes between fourth legs and into two broad elevated areas between fifth pair; sternum of segment 6 recessed slightly between seventh legs. Postgonopodal sterna a modification of bilobed variation discussed by Hoffman (1965); elevated behind stricture, interrupted by transverse groove behind first pair of legs, with distinct medial vertical groove on segments 8-10, becoming shallower, rounded, and less distinct on segment 11; acute subcoxal spines subtending both pairs of legs on segments 8-11, becoming indistinct at anterior legs on segment 12 and gradually more plate-like behind posterior legs of each segment. Hypoproct rounded; paraprocts with edges strongly thickened. Coxae generally without spines, low blunt tubercles present on legs 15-25; prefemoral spines distinct on legs 6-30, indistinct on first five legs; tarsal claws bisinately curved.

Gonopodal aperture subelliptical, narrowing slightly dorsolaterad, about 4.5 mm wide and 2.4 mm long at midpoint; margins raised, slightly thickened along caudal edge. Gonopods (Figs. 1, 7) large, extending forward just beyond anterior edge of aperture, not overlapping. Coxa massive. Prefemur small; enormous prefemoral process arising on dorsal side of prefemur, subglobose basally, widest just proximal to midlength and blackened along inner edge, bent ventrad at about $\frac{2}{3}$ length and tapered to acuminate tip, not bifurcate; tip directed toward midpoint of curve of telopodite, extending beyond apex of telopodite. Telopodite with proximomedial edge expanded into deeply notched plate, basalmost projection enlarged into wedgelike structure; telopodite curved broadly anteriorly distal to expansion, distalmost point at approximately same level as outermost point in curvature of prefemoral process; with subapical lobes on each side, lateral thick and pointed, larger than medial, latter thin and rounded; solenomerite short and blunt, bent caudad, length subequal to lateral lobe, longer than medial lobe; raised ridge with tuberclelike projection about $\frac{1}{4}$ length along inner curvature of telopodite marking course of prostatic groove; groove running mostly along lateral edge of ridge, crossing over from medial side near base of prefemoral process.

Male paratypes.—The W/L ratios of the eight male paratypes range

from 22.0%–22.8%. All specimens display the stripe along the anterior edge of the collum and prominent sternal processes between the third pair of legs. The postgonopodal sterna vary little from the condition in the holotype. On the gonopods, the configuration of the proximomedial expansion varies, but the basalmost projection is always the largest. The tuberclelike projection of the ridge along the inner face of the telopodite also varies, being low, rounded, and virtually absent on some individuals, and sharply pointed and spiniform on others. The prefemoral processes are remarkably similar; the relative thickness of the basal subglobose portion varies slightly, and some are bent ventrad more sharply than others.

Female paratypes.—The five female paratypes agree closely with the males in body proportions, except that they have a higher depth/width ratio, the average being 71.5%. Three individuals lack the yellow stripe along the anterior edge of the collum. The sternal process between the third pair of legs (Fig. 12) is much smaller than those of males, being completely divided and shorter than the width of the adjacent coxae. Only a pair of subcoxal spines is present between the fourth legs; the sterna on segments 5–7 are as on segments 8–10 of the holotype. On the cyphopods (Fig. 16), the medial enlargement of the membrane is very large and conspicuous, and contains darkened inclusions. The receptacle appears striate and extends almost completely around the valves. The latter are small, subequal, and closely adhered together; the operculum is minute and concealed under the free end of the valves.

Variation.—The paranotal color of this species is bright lemon yellow on all but two individuals, a male and female from Union Co., S.C., which displays an orange tint. The stripe along the anterior edge of the collum may be present or absent, but when present is usually broad. As noted earlier, all nine males and two of the five females of the type-series possess the stripe, whereas it is absent from two females. In a large, randomly collected sample of 35 adults (27 ♂♂, 8 ♀♀) from Chester Co., S.C., the stripe is absent from 22 males and all eight females. Thus, only 18.5% of the males and 14.3% of the total sample possess this trait, which is a rough indication of its frequency in the general population at this site. In addition to the stripe along the anterior edge of the collum, a few individuals also possess thin, faint stripes along the caudal edges of the metaterga of segments 1–4. These stripes are only present on individuals which also display the one along the anterior edge of the collum.

The body proportions of the holotype and male paratypes were recorded earlier. A table summarizing the dimensions of the sample from Chester Co. is given below. The remainder of the non-sexual characters are as described for the holotype.

N	W (mm)		L (mm)		W/L (%)	
	Range	\bar{x}	Range	\bar{x}	Range	\bar{x}
Males 27	9.9–12.2	11.1	39.9–51.6	46.0	21.1–24.8	22.5
Females 8	10.5–11.6	11.1	46.3–51.3	48.1	22.4–25.1	23.1

The gonopods are remarkably constant, the most notable variation being the degree of jaggedness of the proximomedial expansion and the prominence of the projections of the mid-telopodite ridge. The males from Chester Co. differ, however, in having much thinner prefemoral processes which are not subglobose basally (Fig. 2). This variation does not have any geographical significance and seems to be characteristic of this particular population.

Ecology.—The type specimens were collected from a seepage area along a small feeder stream to Kings Creek on a rocky hillside in a climax deciduous forest (elevation approximately 1,000 ft). Though a hot, dry August day, the site was comparatively cool and moist, and deep piles of leaves had accumulated beside some of the larger boulders. Several individuals were discovered under these leaf piles, while others were found under small logs or moving across the ground. The species appeared to be abundant, and more material could have been secured. It was not encountered at several other localities in the Kings Mountain area, even though the habitats are similar to the type locality. This site was revisited in late November, 1975, and April, 1976, but no specimens were found.

The South Carolina specimens were also taken during hot, dry August weather and were especially abundant in the predominantly hardwood forest at the Chester Co. site, along the Broad River.

Distribution.—*Croatania catawba* is known from the south-central Piedmont of North Carolina and the north-central Piedmont of South Carolina (Fig. 17). Specimens have been examined as follows:

North Carolina: Lincoln Co., 7.3 mi W Lincolnton, 1♂, 25 October 1952, L. Hubricht (RLH). Cleveland Co., 1.2 mi SE Kings Mountain (town), along I-85 at KOA campsite, 5♂, 1♀, 6 juvs., 10 July 1976. M. Filka and W. W. Thomson (A1049); and 5.8 mi S Kings Mountain (town), along co. rd. 2245, 0.1 mi N jct. co. rd. 2288, 9♂, 5♀, R. M. Shelley and J. C. Clamp (A540) TYPE-LOCALITY. Gaston Co., 4.8 mi SW Gastonia, along co. rd. 1131, 2.1 mi NW jct. co. rd. 1133, 1♀, M. Filka and W. W. Thomson (A1340).

South Carolina: York Co., Kings Mountain State Park, 3♂, 3♀, 20 August 1976, R. M. Shelley (A1416). Chester Co., 13.6 mi W Chester, Woods Ferry Recreation Center, campsite on Broad River in Sumter National Forest, along U.S. Forest Service rd. 574, 3.0 mi W jct. S.C. Hwy.

49, 27♂, 8♀, 2 juvs., 4 August 1976, R. M. Shelley (A1414). Union Co., 12.3 mi SE Union, along S.C. Hwy. 121-72 at crossing Cane Cr., 4♂, 7♀, R. M. Shelley (A1415).

Croatania saluda, new species

Figs. 3, 8, 13

Type-specimens.—Male holotype and nine male and one female paratypes collected by R. M. Shelley, 9 August 1976, from viny undergrowth near Chiles Branch Creek, along S.C. Hwy. 48, 0.1 mi W junction S.C. Hwy. 63, edge of Sumter National Forest, 12 mi S Greenwood, Greenwood Co., S.C. (A1422). Male paratypes deposited in Florida State Collection of Arthropods, Zoologisch Museum Amsterdam, and personal collection of Richard L. Hoffman.

Diagnosis.—Paranota red, with red stripe of varying width along anterior edge of collum; sternal process between third pair of legs of males longer than width of adjacent coxae, bent anteriorly distally, divided apically; gonopods with following characteristics: prefemoral process broadly curved ventrad, apically bifurcate, medial component longer than lateral; expansion of proximomedial edge of telopodite relatively long, irregularly notched; arc of telopodite relatively short and high; subapical lobes of telopodite moderate in size, distinct; solenomerite longer than lateral lobe; distal extremity of telopodite extending beyond outermost point in curvature of prefemoral process.

Holotype.—Length 46.0 mm; width of segment six 10.1 mm, of segment ten 10.3 mm, of segment fifteen 9.6 mm; W/L ratio 22.4%; depth/width ratio 58.3%.

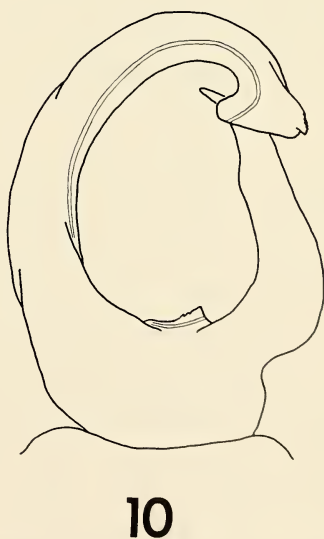
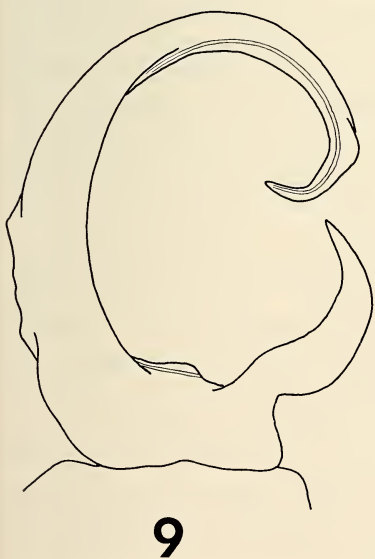
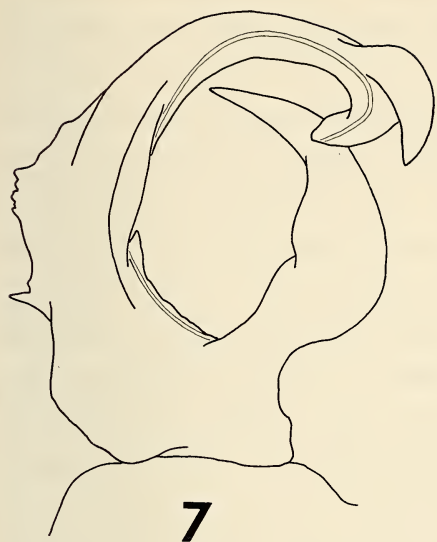
Color in life.—Paranota red, metaterga black; broad red stripe along anterior edge of collum, connecting with paranotal spots; narrow red stripe along caudal edge of collum, faint red stripe along caudal edge of second metatergite. Epicranium, genae, and frons black, epicranial suture and clypeus lighter; antennae dark brown. Venter and legs generally light brown, sterna and basal podomeres of segments 6–15 darker.

Structural details similar to those of *C. catawba* with following exceptions:

Width across genal apices slightly narrower, 4.6 mm; genae distinctly impressed.

Paranota relatively flat. Peritremata more distinctly elevated, resulting in blunt paranotal corners on segments 2–4. Ozopores conspicuous, opening dorsolaterad.

Sternal process between third pair of legs (Fig. 13) bent anteriorly distally, longer than width of adjacent coxae; lobes between fourth pair of legs more prominent than in *C. catawba*; sternum of segment 6 broader



Figs. 7-10. Telopodites of left male gonopods of *Croatania* spp. holotypes, lateral views. 7, *C. catawba*. 8, *C. saluda*. 9, *C. simplex*. 10, *C. yemassee*.

and more deeply recessed between seventh legs. Postgonopodal sterna less obviously bilobed, more platelike; subcoxal spines completely absent. Coxal tubercles present on legs 18–25; prefemoral spines distinct on legs 7–30.

Gonopods (Figs. 3, 8) not overlapping, extending forward just beyond anterior edge of aperture, inserting into depression of sternum between seventh pair of legs. Coxa smaller than in *C. catawba*. Prefemoral process not globose basally, broadly curved ventrad, bifurcate apically, medial component longer than lateral component, width at base of bifurcation subequal to that at base of process, tip extending beyond apex of telopodite. Expansion of proximomedial edge of telopodite longer and more irregularly notched than in *C. catawba*; telopodite more highly arched, distalmost point extending beyond outermost point in curvature of prefemoral process; subapical lobes reduced in size, more distinctly separated from solenomerite than in *C. catawba*, solenomerite longer than lateral lobe; ridge along inner face of telopodite low, indistinct, without projections; course of prostatic groove as in *C. catawba*.

Male paratypes.—The W/L ratios of the nine male paratypes range from 22.1%–24.6%, average 23.3%. All specimens display a red stripe of varying width along the anterior edge of the collum. Two individuals with narrow stripes also have narrow paranotal markings covering little more than the peritremata on the midbody segments. On the holotype and other paratypes, the red color covers the entire paranotum and extends inward along the caudal edge of the metaterga. On the gonopods, the degree of jaggedness of the proximomedial expansion of the telopodite varies, and no two are alike, not even on the same individual. The relative lengths of the two components of the prefemoral process also vary, although the medial one is always longer.

Female paratype.—Length 40.0 mm, width 9.9 mm, W/L ratio 25.0%, depth/width ratio 70.0%. The specimen displays a broad red stripe along the anterior edge of the collum and wide paranotal markings. The sternal process between the third pair of legs is as in *C. catawba*. On the cyphopods, the membrane enlargement is smaller than that of *C. catawba*, and the receptacle, valves, and operculum are as in the type species.

Variation.—Variation throughout the range of *C. saluda* is essentially like that discussed above for the paratypes. The length of the proximomedial expansion varies and is shortest on a male from Edgefield Co., 11.3 mi NW Edgefield (A1418). The degree of separation of the solenomerite and lateral lobe (as viewed medially) is narrowest in specimens from Edgefield and McCormick counties, at the southern edge of the range. The length of the solenomerite relative to the lateral lobe varies, but the former is always longer. A few individuals have projections on the ridge carrying the prostatic groove, but these are generally absent.

Ecology.—This species is abundant in August throughout its range and is usually encountered under thin layers of leaves near water sources. It was taken from predominantly pine forests and some that were predominantly hardwood. The type specimens were collected from an area covered with honeysuckle (*Lonicera* sp.) and low-growing vines, a habitat that is rarely investigated by diplopod collectors.

Distribution.—*Croatania saluda* is known from the central and south-central Piedmont of South Carolina, from Newberry Co. to the Savannah River (Fig. 17). Specimens have been examined as follows:

South Carolina: Newberry Co., 11.7 mi NE Newberry, along S.C. Hwy. 81 at Enoree R., 2♂, 4♀, 5 August 1976, R. M. Shelley (A1419); 9.3 mi NE Newberry, Mollys Rock Picnic Area, Sumter National Forest, 4♂, 3♀, 5 August 1976, R. M. Shelley (A1424); and 9.4 mi NW Newberry, along S.C. Hwy. 32 at Indian Cr., 11♂, 4♀, 5 August 1976, R. M. Shelley (A1420). Greenwood Co., 4.2 mi E Ninety Six, near Wilson Cr., 1♂, 21 May 1960, L. Hubricht (RLH); 12 mi S Greenwood, viny undergrowth area along Chiles Branch Cr., along S.C. Hwy. 48, 0.1 mi W jct. S.C. Hwy. 63, edge of Sumter National Forest, 10♂, ♀, 9 August 1976, R. M. Shelley (A1422) TYPE-LOCALITY; and 12 S Greenwood, unnumbered rd. at Cuffytown Cr., edge of Sumter National Forest, 2♂, 3♀, 9 August 1976, R. M. Shelley (A1423). Edgefield Co., 11.3 mi NW Edgefield, along S.C. Hwy. 283 at Turkey Cr. near McCormick Co. line, 8♂ 6♀, 8 August 1976, R. M. Shelley (A1418); and 11.4 mi W Edgefield along S.C. Hwy. 68, 0.2 mi N jct. S.C. Hwy. 52, ♂, 4♀, 8 August 1976, R. M. Shelley (A1421). McCormick Co., 4 mi E McCormick, along U.S. Hwy. 378 at Hard Labor Cr., ♂, ♀, 8 August 1976, R. M. Shelley (A1425).

Remarks.—The gonopod of *C. saluda* is superficially similar to that of *C. catawba* but differs in several important features, the most obvious being the prefemoral process, which is apically bifurcate in the former and simple in the latter. This structure is also more broadly curved in *C. saluda* and much thicker (subglobose) basally in *C. catawba*. On the telopodite, the expansion of the proximomedial edge is longer and more irregularly notched in *C. saluda* and subequal in length to the prefemoral process on some individuals. In the type species the expansion is always shorter than the length of the prefemoral process and usually consists of two main groups of notches, one at either end. The arc formed by the curvature of the telopodite is longer and broader in *C. catawba*, although this difference is not readily apparent in the holotypes. The subapical lobes are much larger in *C. catawba*, but the solenomerite is more distinctly separated from the lateral lobe in *C. saluda*. In the latter species the solenomerite is longer than the lateral lobe, whereas in *C. catawba* they are either subequal, or the solenomerite is shorter.

The two species can also be distinguished by non-sexual characters, and

the yellow and red paranotal colors afford a ready basis for field identifications. The paranotal corners of segments 2-4 are more blunt in *C. saluda* due to thicker peritremata on these segments. Ventrally, the sternal processes on the fourth segments are similar in both species, but the post-gonopodal sterna are flatter and more platelike in *C. saluda*. The depression in the sternum between the seventh legs is deeper and broader in *C. saluda*.

Croatania simplex, new species

Figs. 4-5, 9, 14

Type-specimens.—Male holotype (A1417) and fourteen male and seven female paratypes collected by R. M. Shelley, 4 August 1976, from Chester State Park, Chester Co., S.C. Male and female paratypes deposited in Florida State Collection of Arthropods, Zoologisch Museum Amsterdam, and personal collection of Richard L. Hoffman.

Diagnosis.—Paranota yellow, with or without yellow stripe along anterior edge of collum; sternal process between third pair of legs of males shorter than width of adjacent coxae, straight, divided at midlength; gonopods with following characteristics: prefemoral process short, terminating well below level of tip of telopodite, usually of subequal thickness and without apical bifurcation; expansion of proximomedial edge of telopodite relatively shallowly notched; subapical lobes of telopodite greatly reduced, indistinct; solenomerite elongate and broadly curved toward center of arc of telopodite, acuminate, much longer than lateral lobe; distal extremity of telopodite extending slightly beyond outermost point in curvature of prefemoral process.

Holotype.—Length 43.7 mm; width of segment six 10.6 mm, of segment ten 10.7 mm, of segment fifteen 10.2 mm; W/L ratio 24.5%; depth/width ratio 57.0%.

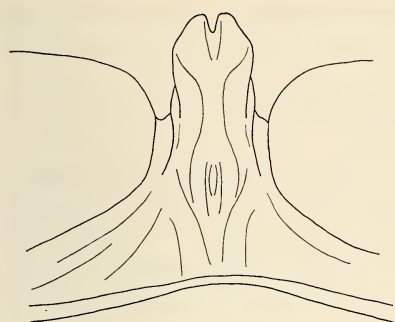
Color in life.—Paranota bright lemon yellow, metaterga black; broad yellow stripe along anterior edge of collum, connecting with paranotal spots. Epicranium and interantennal region black, genae and clypeus lighter; antennae brown. Venter and legs essentially uniform in color, lighter than paranota.

Structural details similar to those of *C. catawba* with following exceptions:

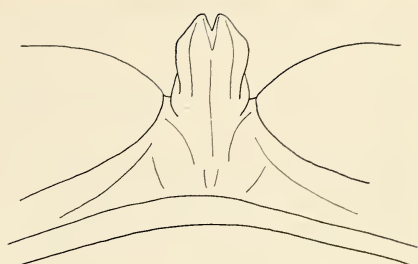
Width across genal apices slightly narrower, 5.0 mm; genae distinctly impressed.

Paranota relatively flat. Peritremata slightly more distinct on segments 2-4, resulting in less rounded paranotal corners.

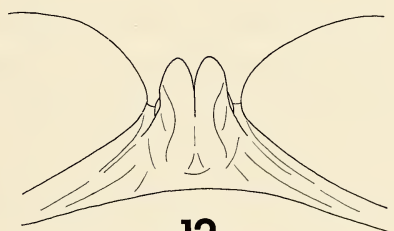
Sternal process between third pair of legs (Fig. 14) divided at midlength, leaning anteriorly but straight, not bent distally, shorter than width



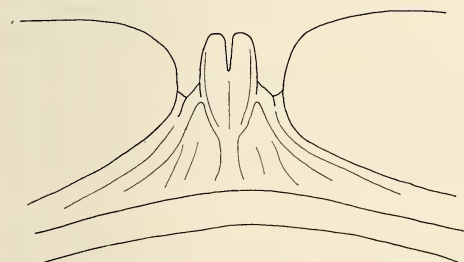
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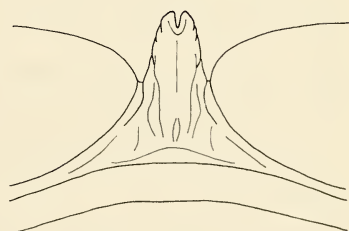
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15

Figs. 11–15. Median sternal processes of fourth segments (between third pairs of legs) of *Croatania* spp., caudal views. 11–12, *C. catawba*; 11, Holotype; 12, Female paratype. 13, *C. saluda*, holotype. 14, *C. simplex*, holotype. 15, *C. yemassee*, holotype.

of adjacent coxae; sternum more deeply and broadly recessed between seventh legs; postgonopodal sterna less obviously bilobed, more plate-like, subcoxal spines absent except for small pair on segment 8. Coxal tubercles present on legs 13–27; prefemoral spines distinct on legs 5–30.

Gonopods (Figs. 4, 9) overlapping at distal curvature, extending beyond anterior edge of aperture and inserting into indentation of sternum be-

tween seventh legs. Prefemoral process greatly reduced, not globose basally, broadly curved ventrad, terminating well below level of tip of telopodite. Expansion of proximomedial edge of telopodite with shallow notches; distal curvature of telopodite slightly higher than in *C. catawba*, distal-most point extending slightly beyond outermost point in curvature of prefemoral process; subapical lobes greatly reduced, inconspicuous, medial lobe almost nonexistent, lateral lobe slightly larger; solenomerite elongate and broadly curved, acuminate, extending inward beyond tip of prefemoral process, much longer than lateral lobe; ridge along inner face of telopodite indistinct, without projections, course of prostatic groove as in *C. catawba*.

Male paratypes.—The W/L ratios of the fourteen male paratypes range from 21.5%–24.5%, average 22.8%. Three individuals lack the stripe along the anterior edge of the collum. Two have an orange tint to the paranotal markings which extend inward on one suggesting a stripe along the caudal edge of the metaterga. On the gonopods, the prefemoral processes vary in several respects. Some are broadly curved, whereas others are relatively flat. The structure is apically bifurcate on two specimens, with medial component longer and more prominent than the lateral one (Fig. 5). It is subglobose basally on others. The subapical lobes, especially the medial one, are more pronounced on most paratypes than on the holotype, and the solenomerite is slightly bisinuate on some specimens.

Female paratypes.—The seven female paratypes have a higher W/L ratio than the males, the average being 24.6%. Two individuals lack the yellow stripe along the anterior edge of the collum. The sternal process between the third pair of legs is reduced from the condition in *C. catawba*. On the cyphopods, the membrane enlargement is smaller than that of *C. catawba*, and the receptacle, valves, and operculum are as in the type species.

Ecology.—This species is extremely abundant at the type-locality. Most individuals were found under thin leaf cover in predominantly hardwood areas on slopes near creeks or along the edges of paths, and were taken in association with *Sigmoria latior* intergrades (see Shelley 1976).

Distribution.—Known only from the type-locality.

Remarks.—*Croatania simplex* is distinct from its congeners in the greatly reduced subapical lobes of the telopodite, elongate solenomerite, and short prefemoral process. The sternal process of the fourth segment is also unique, being shorter than the margins of the adjacent coxae and divided for a greater proportion of its length, beginning at midpoint. The species resembles *C. catawba* in the yellow paranotal color and the tendency of the prefemoral process to be subglobose basally. It is similar to *C. saluda* in the arc of the telopodite, the solenomerite's being longer

than the lateral lobe, and the tendency of the prefemoral process to be bifurcate.

Croatania yemassee, new species

Figs. 6, 10, 15

Type-specimens.—Male holotype collected by L. Hubricht, 20 September 1959, from low oak woods, 8 mi S Hardeeville, Jasper Co., S.C. (RLH). Male and female paratypes collected by L. Hubricht, 5 July 1959, from a small island 7 mi E Frogmore, Beaufort Co., S.C. (RLH).

Diagnosis.—Sternal process between third pair of legs of males straight, subequal to or slightly longer than width of adjacent coxae, divided apically; gonopods with following characteristics: prefemoral process bisinuately curved, bent sharply ventrad near acuminate tip; expansion of proximo-medial edge of telopodite reduced, with only small denticulations; arc of telopodite short and high; subapical lobes reduced, indistinct; distal extremity of telopodite extending beyond outermost point in curvature of prefemoral process.

Holotype.—Length 40.9 mm; width of segment six 10.5 mm, of segment ten 10.7 mm, of segment fifteen 10.4 mm; W/L ratio 26.2%; depth/width ratio 46.7%.

Color in life unknown, evidence of stripe along anterior edge of collum in preserved specimen.

Structural details similar to those of *C. catawba* with following exceptions:

Width across genal apices slightly narrower, 4.7 mm. Antennae longer, extending slightly beyond caudal edge of third metatergite. Genae with medial impression. Frontal setae not detected and presumed absent.

Peritremata more distinctly elevated, resulting in blunt paranotal corners on segments 2–4. Ozopores more conspicuous, opening dorsolaterad.

Sternal processes between third pair of legs (Fig. 15) straight, not bent anteriorly distally, divided apically, slightly longer than width of adjacent coxae; lobes between fourth pair of legs more prominent than in *C. catawba*; sternum between seventh legs deeply recessed. Postgonopodal sterna less obviously bilobed, more platelike; subcoxal spines subtending only posterior legs on segment 8, absent thereafter. Coxal tubercles present on legs 8–27; prefemoral spines distinct on legs 5–30.

Gonopods (Figs. 6, 10) not overlapping, extending forward just beyond anterior edge of aperture. Prefemoral process upright, bisinuately curved, not globose basally, bent ventrad apically and narrowing abruptly to acuminate tip, tip directed toward midpoint of telopodite. Expansion of proximo-medial edge of telopodite reduced, with only small denticulations; telopodite highly arched and bent abruptly dorsad, distal extremity extending beyond outermost point in curvature of prefemoral process; subapical

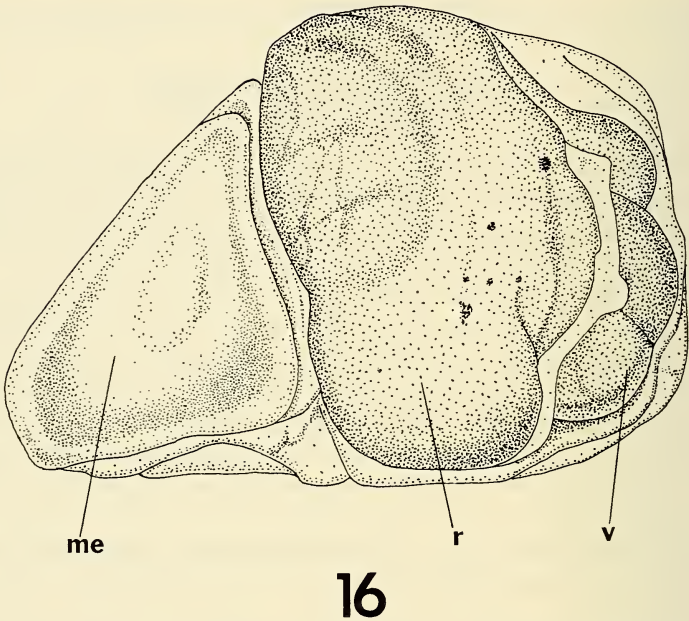


Fig. 16. Left cyphopod of female paratype of *C. catawba*, ventral view, *in situ*. me, membrane enlargement; r, receptacle; v, valves.

lobes reduced, inconspicuous, lateral lobe subquadrate, serrate; solenomerite blunt, at approximately same level as distal portion of prefemoral process; ridge along inner face of telopodite not distinctly raised, with basal projection; course of prostatic groove as in *C. catawba*.

Male paratype.—The male paratype is badly fragmented and cannot be measured but agrees essentially with the holotype in all structural details. On the gonopods, the prefemoral process is more pointed, and the expansion of the proximomedial edge of the telopodite is more distinctly notched.

Female paratype.—Length 44.6 mm, greatest width 11.4 mm, W/L ratio 25.6%, depth/width ratio 66.7%. Color in life unknown, but there is evidence of a stripe along the anterior edge of the collum. Frontal setae are apparently absent, and the sternal process between the third pair of legs is as in *C. catawba*. On the cyphopods, the membrane enlargement is reduced over the condition in *C. catawba*, and the receptacle, valves, and operculum are as in the type-species.

Distribution.—Coastal islands and outer Coastal Plain of southern South Carolina (Fig. 17). Specimens have been examined as follows:

South Carolina: Jasper Co., low oak woods, 8 mi S Hardeeville, ♂, 20

September 1959, L. Hubricht (RLH) TYPE-LOCALITY. Beaufort Co., small island 7 mi E Frogmore, ♂, ♀, 5 July 1959, L. Hubricht (RLH).

Remarks.—*Croatania yemassee* is distinct from its congeners in the apparent loss of frontal setae, the bisinuate curved prefemoral process, and reduction in the expansion of the proximomedial edge of the telopodite. The depression in the sternum between the seventh legs is also much deeper than in the other species. Other than the diagnostic characters of the genus, it has little in common with *C. catawba* but is similar to *C. saluda* in the height and breadth of the arc of the telopodite, the relatively flattened postgonopodal sterna, and the blunt paranota of segments 2–4. The reduction in the subapical lobes of the telopodite, a feature shared with *C. simplex*, is an example of convergence and not taxonomically significant.

Ecology

A striking ecological characteristic of *Croatania* is the abundance of its species in July and August, the hottest, driest, months of the year. The millipeds seem to thrive in such conditions, when many other species are scarce (see Shelley, 1976, for a comment on the effects of climate on *Sigmoria latior*). Other diplopods that would be expected in the Piedmont, such as species of *Cambala*, *Polyzonium*, *Pseudopolydesmus*, *Ptyoiulus*, and *Scytonotus*, were notably absent in August 1976, presumably because of the harsh conditions. *Croatania catawba* and *C. saluda* were frequently found in association with *Pachydesmus crassicutis incurtus*, which is common in the same habitats (Shelley and Filka 1977). In addition to these xystodesmids, *Sigmoria latior* intergrades, *S. l. hoffmani* Shelley, and two undescribed forms currently under study, the only diplopods that were even moderately abundant in the Carolina Piedmont in August 1976 were *Narceus americanus* (Beauvois) and *Abacion magnum* (Loomis).

Croatania is also unusual in the variety of habitats it occupies. In the Kings Mountain region it occurs in climax deciduous forests with thick leaf layers, traditional xystodesmid habitat. Outside this region, however, it inhabits intermediate successional stages of mixed pine-hardwood and was found in some localities dominated by pine. At Mollys Rock Picnic Area, Newberry Co., South Carolina, for example, several individuals of *C. saluda* were discovered under pine bark mulch on a walkway through a pine forest. At the type-locality of *C. saluda*, individuals were found in a pine area covered with honeysuckle and low-growing vines, a habitat that would usually be bypassed by milliped collectors. These two localities were somewhat atypical, and in most places *Croatania* occurred under thin leaf layers relatively close to water sources. Sites with moderate slopes leading to rivers or creeks usually produced both *Croatania* and *Pachydesmus* at the bases of the slopes. As with *P. c. incurtus* (Shelley and Filka

1977), specimens of *Croatania* from the Kings Mountain region are notably larger and more robust than those from areas farther south with a greater proportion of pine, probably a reflection of more favorable environmental conditions in this region.

Distribution

The distribution of *Croatania* (Fig. 17) is of interest in the absence of obvious geographical or ecological interpretations. Discounting *C. yemassee*, which is isolated on the southeastern coast of South Carolina, the ranges of the other three species in the state cannot be correlated with any factor; they all occur in the same general area of the central Piedmont and in essentially the same habitats. The Savannah River is perhaps the southern boundary for *C. saluda* (to be determined by future field work in Georgia), but there is no ready geographical explanation for its apparent northern limit. It was collected as far north as the Enoree River, but its range is bisected by the much larger Saluda River. Likewise, *C. catawba* was collected as far south as the Tyger River, but its range is bisected by the much larger Broad River. Current data indicate that the ranges of these two species abut near the Enoree and Tyger Rivers and the Union-Newberry Co., S.C., line. Further collecting may show that they overlap. Since the ranges of both species span several relatively large rivers, it seems that stream capture and resultant changes in drainage boundaries may have been important factors in determining their present distributions. Comment on *C. simplex*, known from only one locality, is deferred until its complete range can be more precisely defined.

The distribution of *C. catawba* in North Carolina can perhaps be explained geographically. According to Stuckey (1965), the Kings Mountain range of Cleveland and Gaston counties continues northward through a series of hills and ridges to Anderson's Mountain in Catawba Co., just north of Lincoln Co. Perhaps the distribution of *C. catawba* in North Carolina is associated with this physiographic feature, and if so, it should occur in Catawba Co. and the northern part of Gaston Co. Efforts to find the milliped in these areas have so far been unsuccessful but remain an objective of future studies.

Relationships

Generic.—The presence of large sternal processes on the fourth segments, bilobed postgonopodal sterna, and similarities in the distal portions of the telopodites, indicate a close relationship between *Croatania* and *Cleptoria*. The former is a more advanced, specialized genus as evidenced by the more highly developed prefemoral process, ornate proximomedial expansion of the telopodite, and subapical lobes. In *Cleptoria* the pre-



Fig. 17. Distribution of *Crotania* in North and South Carolina.

femoral process is either lacking or greatly reduced and subtriangular, and the other two structures are absent, except for a subapical lateral lobe on *C. abbotti* Hoffman.

Hoffman (1963) suggested that *Lyrranea*, *Dynoria*, *Cleptoria*, and *Stelgipus*, all lowland xystodesmid genera, had enough common features to be worthy of tribal distinction. He cited five characteristics which set them apart from other xystodesmids but stopped short of formally erecting such a tribe. *Crotania* possesses these same traits and would belong to the same tribe, as would two additional undescribed genera in the NCSM collection from piedmont South Carolina. Thus, the lowland regions of the southeastern United States harbor an assemblage of related xystodesmids, and further investigations are needed on the fauna of this area to fully determine whether a suprageneric taxon is warranted.

Specific.—Three evolutionary trends are evident in *Crotania*, all emanating from the condition in *C. saluda* (Fig. 18), and the morphological and geographical evidence suggest that the genus originated in the McCormick Co. area near the Savannah River and spread in three separate lines, either concurrently or at different times, in the directions of the derived species. Expansion in a northerly direction, accompanied by enlargement of the subapical lobes of the telopodite, broadening of its arc, and basal thickening of the prefemoral process, resulted in *C. catawba*. Expansion in a northeastwardly direction, accompanied by reduction in

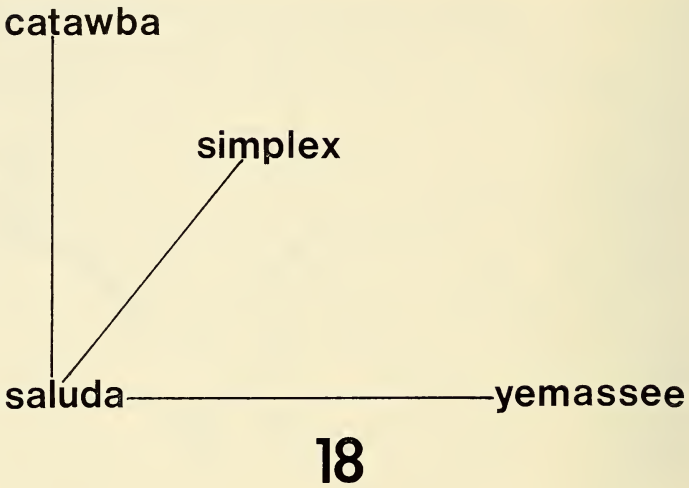


Fig. 18. Relationships in the genus *Croatania*.

the subapical lobes of the telopodite and prefemoral process, and elongation of the solenomerite, produced *C. simplex*. Finally, expansion in a south-eastwardly direction, accompanied by reduction in the subapical lobes and proximomedial expansion of the telopodite, and narrowing and heightening its arc, yielded *C. yemassee*. Loss of bifurcation of the prefemoral process is common to all three lines. Consequently, *C. saluda* is viewed as the pivotal species in *Croatania*, and the other species are all more closely related to it than to each other. As indicated earlier, *C. simplex* is unique in lacking both a large prefemoral process and distinct subapical lobes. However, its relationship to *C. saluda* is revealed by the occasional appearance of bifurcation in the prefemoral process and lengthening of the solenomerite, which is longer than the lateral lobe in both species. The reduced subapical lobes of both *C. simplex* and *C. yemassee* are attributed to convergence, each being derived independently from the condition in *C. saluda*. Due to the much greater variability of the prefemoral process and the unique configuration of the solenomerite, *C. simplex* is considered to be the most recently evolved, having not yet attained the phenotypic (and presumably genotypic) stability of the others.

Croatania seems to be a relatively old genus, as evidenced by the occurrence of three species, *C. catawba*, *C. simplex*, and *C. saluda*, within a few miles of each other in an area lacking obvious geographical or environmental isolating factors. These forms are all reproductively isolated, and intergrade populations that at one time must have linked *C. saluda* to the others have disappeared. *Croatania catawba*, moreover, has existed

long enough to have spread all the way to Lincoln Co., in south-central North Carolina. Additional field work in piedmont South Carolina could conceivably disclose still more forms, and future efforts should be focused in a northwestwardly direction, towards Greenville, Laurens, and Spartanburg counties. The Piedmont of Georgia should also be examined to see if additional species of *Croatania* occur south of the Savannah River.

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